

# The Composition of the Bee (Apoidea: Hymenoptera) Fauna Visiting Flowering Trees in New South Wales Lowland Subtropical Rainforest Remnants

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WILLIAMS, G.A. AND ADAM, P. (1997). The Composition of the Bee (Apoidea: Hymenoptera) Fauna Visiting Flowering Trees in New South Wales Lowland Subtropical Rainforest Remnants. *Proceedings of the Linnean Society of New South Wales* **118**: 69–95

Native and exotic bees were sampled visiting mass-flowering rainforest trees in lowland subtropical rainforest remnants in the Manning Valley, on the New South Wales north coast. The number of bee species varied between individual rainforest sites and native bee taxa exhibited differential occurrence at individual plant species and in different rainforest subformations. Bees exhibited increased recruitment responses to peak-phase flowering of individual trees. Flowers visited by bees exhibited a number of different floral morphologies. Colletidae-Hylaeinae was the most diverse native bee group collected but individual taxa were in general not restricted to single plant species. Exotic *Apis mellifera* were most abundant at flowers during peak-phase flowering. *Apis mellifera* foraged at most plants sampled and foraging activities resulted in disturbance to small native hylaeine bees on flowers. Native *Trigona carbonaria* bees were recorded on fewer species of flowering trees than was *Apis mellifera*.

Manuscript received 24 Oct 1995, accepted for publication 19 Apr 1996

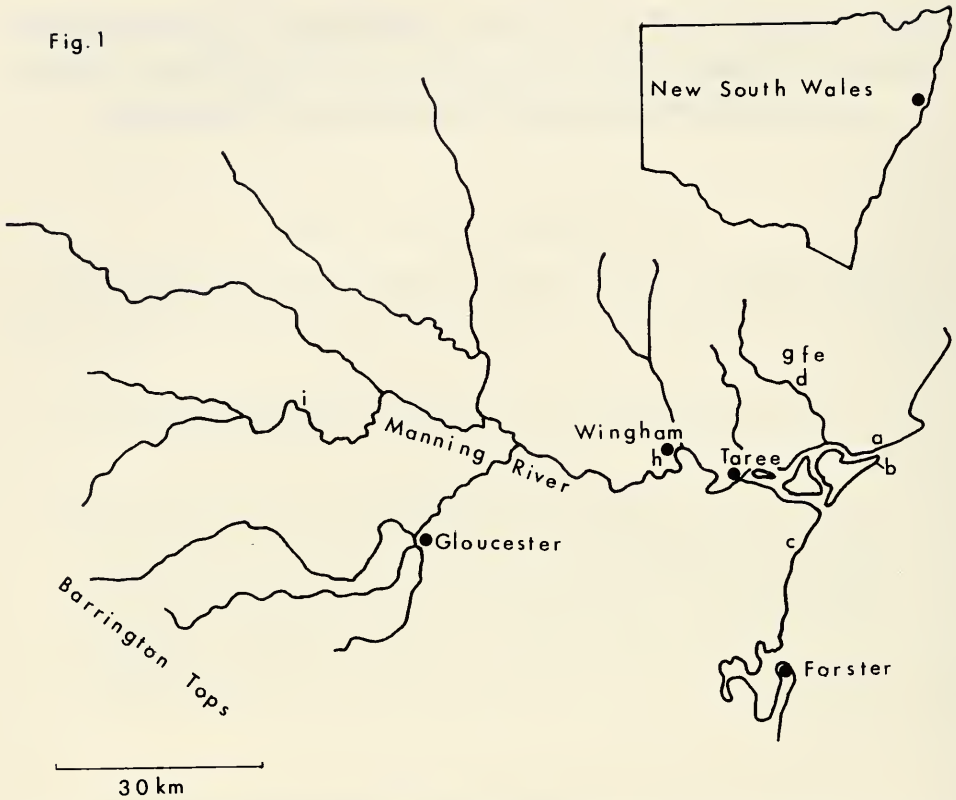
KEYWORDS: Bees, pollination, subtropical rainforest, remnant vegetation, conservation.

## INTRODUCTION

The popular awareness of plant-pollinator interactions is largely focused on the role of 'specialised' bees, especially that of the honey bee *Apis mellifera* (Paton 1993; Seeley 1983), in the pollination of both wild and horticultural plants. However, bees exhibit great ecological diversity as pollinators (Roubik 1989). Bees, and in particular the neotropical Euglossini, have been the subject of numerous pollination ecology studies (e.g., Cruden 1972; Frankie et al. 1976; Armbruster and Webster 1979; Ackerman 1983; Kevan and Lack 1985; Appanah, Willemstein and Marshall 1986; Roubik and Ackerman 1987; Snow and Roubik 1987; Roubik 1989; Armbruster and Berg 1994). Bees are not always pollinators of the various flowering tropical rainforest plants from which bee visitation has been recorded, and may consume nectar and pollen, and destroy flowers, without any benefit to plant reproduction (Bullock 1994; Roubik 1989; Williams and Adam 1994).

Although records exist for bees visiting plants in sclerophyllous habitats (e.g., Exley 1968a, 1968b; Houston 1975, 1981; Armstrong 1979; Houston et al. 1993) little is known about bee-plant interactions in Australian rainforest communities. Gross (1993), however, recorded bee pollination of the pioneer tropical Australian rainforest shrub *Melastoma affine* (Melastomataceae), principally by buzz-pollinating Anthophoridae. Additionally, Heard (1993) recorded native *Trigona* bees pollinating the subtropical rainforest tree *Macadamia integrifolia* (Proteaceae) cultivated as an orchard crop.

The pollination ecology of lowland subtropical rainforest trees was studied, from



*Figure 1.* Study sites (rainforest subformation/class definition incorporates structural-physiognomic classification of Webb [1978]). **a.** Harrington ( $32^{\circ}52'30''\text{S}$ ,  $152^{\circ}41'00''\text{E}$ ) (littoral rainforest; mixed notophyll vine forest). **b.** Manning Point ( $31^{\circ}53'30''\text{S}$ ,  $152^{\circ}40'00''\text{E}$ ) (littoral rainforest; mixed notophyll vine forest). **c.** Saltwater Reserve ( $32^{\circ}00'30''\text{S}$ ,  $152^{\circ}33'45''\text{E}$ ) (littoral rainforest; mixed notophyll vine forest). **d.** Lansdowne Reserve (0.5km SE Lansdowne) ( $31^{\circ}47'30''\text{S}$ ,  $152^{\circ}32'30''\text{E}$ ) (riverine rainforest; notophyll vine forest). **e.** Lorien Wildlife Refuge (3km N. Lansdowne) ( $31^{\circ}45'00''\text{S}$ ,  $152^{\circ}32'30''\text{E}$ ) (submontane rainforest; notophyll-notophyll evergreen vine forest). **f.** Lorien Wildlife Refuge (wet sclerophyll forest). **g.** Kenwood Wildlife Refuge (4km NNW Lansdowne); ( $31^{\circ}44'45''\text{S}$ ,  $152^{\circ}31'30''\text{E}$ ) (submontane rainforest-mixed wet sclerophyll forest). **h.** Wingham ( $31^{\circ}52'40''\text{S}$ ,  $152^{\circ}22'00''\text{E}$ ) (riverine + riparian rainforest; notophyll vine forest/complex notophyll vine forest). **i.** Woko National Park (approximately 24km NNW Gloucester) ( $31^{\circ}49'00''\text{S}$ ,  $151^{\circ}47'00''\text{E}$ ) (riverine + riparian rainforest; notophyll vine forest).

1990 to 1994, in rainforest remnants located in the Manning Valley on the north coast of New South Wales (G. Williams unpubl. data) (Fig. 1). The sites have also been subject to intensive invertebrate surveys, especially since 1979 (Williams 1993). An additional number of rainforest tree species in rainforest-wet sclerophyll forest ecotones were also sampled. This was a broad-based study of the rainforest community primarily designed to investigate the incidence of generalist versus specialist plant-pollinator relationships in subtropical rainforests, and to identify putative pollinators. It resulted in the collection of more than 60,000 insects of which bees formed a small proportion (<5%). Although no attempt was made to measure the efficiency of individual insect species as pollinators (e.g., foraging patterns, pollen deposition and resultant seed set) field observations suggested that insects visiting entomophilous flowers were capable of achieving some level of pollination; irrespective of the pollen loads they were capa-

ble of transporting, the frequency with which they contacted stigmas or the distance that they travelled within plant populations. However, bees are of ecological interest, and the aim of this paper is to describe the bee fauna collected from 17 species of mass-flowering rainforest trees during this study (Table 1). There is morphological variation between the flowers of these species but all conform to the entomophilous flower syndrome (Armstrong 1979; Faegri and van der Pijl 1979). All flowers were open in structure, and readily accessible, with little depth effect in the perianth. Flowers were coloured white, or creamish white, except for those of *Tristaniopsis laurina* which were yellow. None of the flowers possessed obvious nectar guides. Although there was variation in foraging behaviour, temporal and spatial constancy to available blossoms and placement and carriage of pollen on their bodies, most bees appeared to be generalist pollinators. However, further studies are needed to define the pollination ecology of individual bee taxa. Bees were not recorded from 6 understorey and subcanopy trees that have specialised pollination ecologies (*Wilkiea huegeliana*, *Daphnandra micrantha*—Monimiaceae, *Eupomatia laurina*—Eupomatiaceae, *Endiandra muelleri*—Lauraceae, *Rapanea howittiana*, *R. variabilis*—Myrsinaceae). These possess more specialised flowers (except for *D. micrantha*) that generally deny bee access and, with the exception of *E. muelleri* (whose pollinators are unknown), are pollinated by thrips (*W. huegeliana*, *R. howittiana*, *R. variabilis*), weevils (*E. laurina*) or Nematoceran flies (*D. micrantha*) (G. Williams unpubl. data).

There has been no previous systematic collection of the regional rainforest bee fauna. A number of substantial range extensions to previously known distributions are listed in the appendix.

#### STUDY SITES AND METHODS

Most study sites were located in the floodplain, lower valley and maritime zone of the Manning Valley. However, the Woko National Park site is situated in the western extreme of the valley, approximately 80 km inland from the coast. Sites a-h (Fig. 1) ranged from 10–150 metres above sea level but the Woko site (i) was at approximately 300 metres a.s.l.

Definitions of subtropical rainforest follow Adam (1987, 1992). Definitions of riparian, riverine and littoral subtropical rainforest subformations in the Manning region follow Williams (1993). Floristic composition of sites and the regional physical environment are discussed in Williams (1993).

Trees were sampled by hand netting throughout their flowering period. Insects respond positively to increased availability of floral resources (Sands and House 1990; Augspurger 1980) but insect activity is also influenced by temperature, humidity, shading of flowers and foliage, wind and rainfall (Cruden 1972; Stiles 1977; Primack 1978; Wolda 1978; Real 1981; Kevan and Baker 1983; Armbruster and Berg 1984; Matthews and Kitching 1984; Frith and Frith 1985; Inouye and Pyke 1988; Read 1989; Roubik 1989; Basset 1991; Gross 1993). Consequently, sampling was avoided during cool, rainy periods, periods of moderate to strong wind, and in shaded situations (very few Hymenoptera were active on shaded flowers; large insects, generally, were absent)—conditions that reduce insect activity and abundance.

Crown height of the study trees was generally low (normally less than 10m). Inflorescences were sampled using an extendible 6.2m hand held net, with a mouth diameter of 46 cm. A fine nylon, sailcloth re-enforced, net was attached to the net frame. The size of the net mesh prevented escape of insects >0.2 mm. As far as possible, two trees of any single species, from each study site, were sampled each day of collection (between 0900–1500 hrs). This was to maximise the range of anthophilous (flower frequenting) taxa captured during the period of greatest insect activity.



However, flowers of *Acradenia euodiiformis* (Rutaceae) were sampled every two hours from 0800 hrs until 2000 hrs, and weather conditions noted (Table 3), as an investigation of daily fluctuations in numbers of foraging anthophilous insects (this was only intended as a preliminary investigation of foraging patterns). Other species were generally sampled only once in the morning and afternoon, on any collection day. Although there may be variation in the daily cycle of available floral rewards offered by subtropical rainforest trees, *A. euodiiformis* did not appear to deviate from the overall pattern of nectar production by generalist mass-flowering trees included in the study. General insect visitation to individual tree species was also observed, at all sites except Woko, between sunrise and two hours after sunset, for a minimum of 8 hours (range 8->10hrs). Bees were not active at night. Individual trees and tree species failed to flower each year and, consequently, it was not possible to sample each tree species over each of the three seasons (1990-91, 1991-92, 1992-93). However, increased sampling at individual tree species did not necessarily result in increases in the number of bee taxa collected. For example, *Alphitonia excelsa* (Rhamnaceae) sampled ('n', number of samples, =160) at Kenwood Wildlife Refuge in 1992, resulted in the collection of 10 bee species, but *A. excelsa* at Harrington, sampled (n=590) intensively over three seasons (1990-1993), yielded only 7 species (Table 1). The flowering phenology of populations also varied, thus the duplication of samples was an attempt to maximise collection of the visiting insect taxa.

On individual days of collection ten inflorescences from each tree were sampled (randomly across the crown face) by quickly placing the net over individual flower masses and briskly shaking. The net mouth was closed by quickly rotating the handle to minimise loss of fast flying insects. Inflorescence sets were not necessarily resampled each day due to factors such as variation in shading and netting damage to flowers. Collectively, approximately 3,000 inflorescences were sampled by this method during the 1990-91, 1991-92 and 1992-93 study seasons, but the number of samples collected from individual tree species varied between years due to differences in phenology (see Table 2). Insect taxa in samples, collectively, were dominated by Coleoptera, Diptera and Hymenoptera generally; but overall bees (although often conspicuous) were relatively uncommon.

Following the collection of each sample the net bag was detached, placed in a plastic container, sprayed with commercial pyrethroid insecticide and sealed. After 10-20 minutes the contents were emptied into individual labelled containers. These were later sorted separately to remove extraneous floral segments (e.g., stamens, petals), and then freeze-stored in labelled Petri dishes for later counting of numbers of species and individuals, measuring, identification and mounting of representative specimens.

The hand net collection method could not be used during and after heavy rain as wet foliage and flower surfaces quickly saturated the net bag, to which small insects readily adhered. The netting technique was also limited when flowers were sparse or held below foliage. For this latter group of trees (i.e., *Diospyros australis*, *Abrophyllum ornans*) collection using malaise intercept traps (placed on forest margins adjoining or below trees), or hand netting of individual insects as they landed on flowers, was undertaken. No bees were collected in malaise traps set during this study though numerous aculeate wasps were collected by this method. This divergence in trapping methods restricts quantitative comparisons between plant species but does permit a qualitative indication of potential pollination agents. Large insects in general do not behave as inert objects moving in constant and linear patterns, and some large Hymenoptera (e.g., Scoliididae) are able to navigate around malaise intercept traps (Campbell and Brown 1994). Of interest, however, the large halictid bee *Nomia aurantifera* was frequently collected in malaise traps during biological surveys of floodplain rainforest remnants in the Manning Valley (G. Williams unpubl. data) but otherwise was not collected or observed on flowering plant species included in this study.



### Field estimation of recruitment cues and potential floral resources

Anthophilous insects are principally recruited to blossoms by visual and olfactory cues (Williams and Dodson 1971; Proctor and Yeo 1975; Armstrong 1979; Kevan and Baker 1983; Papaj and Prokopy 1989; Bell 1990). Inflorescence movement is also thought to stimulate visual recruitment of insects (Bell 1990).

The measurement of potential floral resource availability at various times in the flowering of individual rainforest plants allows an assessment of the change in recruitment stimulus to pollinators (Kearns and Inouye 1993).

A simple field technique was devised to investigate relationships between abundance and richness of bees and potential resources indicated by numbers of open flowers. The technique entailed an estimation of the blossom (or bud) to leaf surface ratio (BLS) on each of the trees being sampled. The estimation was based on 3 points of reference (left, centre, right) across the horizontal visual field of each plant to be sampled, immediately prior to sampling. These three values were summed and a mean value determined.

Flower or floret opening is rarely synchronous and inflorescences normally consist of fully open flower buds, partially open buds and senescent or fructescent flowers. These patterns are a fundamental and necessary consequence of inflorescence structure. A relative estimate of percentage available buds (PAB) was obtained by counting buds on inflorescence subsections, total bud numbers on individual inflorescences or solitary flowers. Minimum numbers of buds counted ranged from total numbers, for species with large but relatively sparse flowers (i.e., *Rhodomyrtus psidioides*) to more than 300, on a minimum of 10 inflorescences, for species with numerous small flowers (e.g., *Euroschimus falcata*). The available bud (PAB) value is a relative measure, because the finite number of initially available buds gradually diminishes due to carpel development, abortion of flowers or herbivore attack.

Both BLS and PAB values are influenced by environmental cues (e.g., day length, temperature, rain), leaf phenology, herbivore damage, number of florets in the inflorescence, inflorescence structure etc., and are not necessarily constant throughout the period of anthesis. However, the two measures provided a useful, though crude, field estimation of potential floral resources against which to investigate bee recruitment (Tables 2 and 3, Figs 4c and 4d).

Several flaws are inherent to the methods. BLS ratios are estimated horizontally at eye level but a declination estimate would probably yield a higher blossom surface value, and one more approximately comparable to the visual cue perceived by insects in flight. In mass-flowering species such as *Tristaniopsis laurina* (Myrtaceae) the inflorescences are partly obscured by leaves and BLS values are biased in favour of leaf surface. In such instances flowers may actually be obscured to insects. BLS values will never reach 100%, this being a consequence of the presentation of flowers and leaves, so that peak recruitment responses in tabulated data are indicated at BLS values  $\geq 50\%$ .

PAB values may be similarly biased as it is difficult to evaluate values for upper canopy inflorescences.

## RESULTS AND DISCUSSION

### Fidelity of bee taxa to plant species

A summary of the bee species collected is provided in Table 1. We were unable to identify a number of small Euryglossinae collected primarily on flowers of *Waterhousea floribunda* and *Tristaniopsis laurina*. These are not considered in this paper and reference specimens are lodged with the CSIRO, Division of Entomology (Canberra). Records in Table 1 are derived primarily from bees collected in netted samples, but observations of several additional bee species, not collected in samples, are also included











Fig. 2a

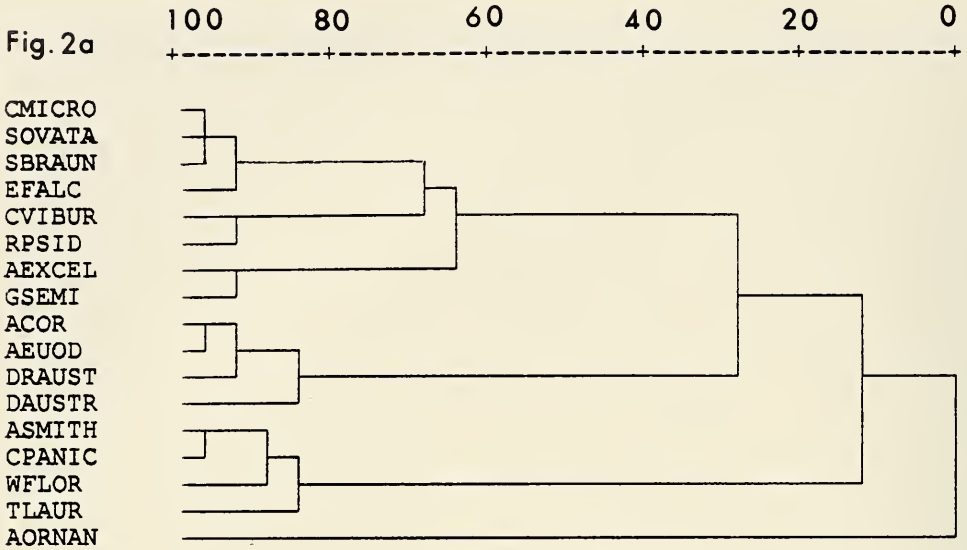
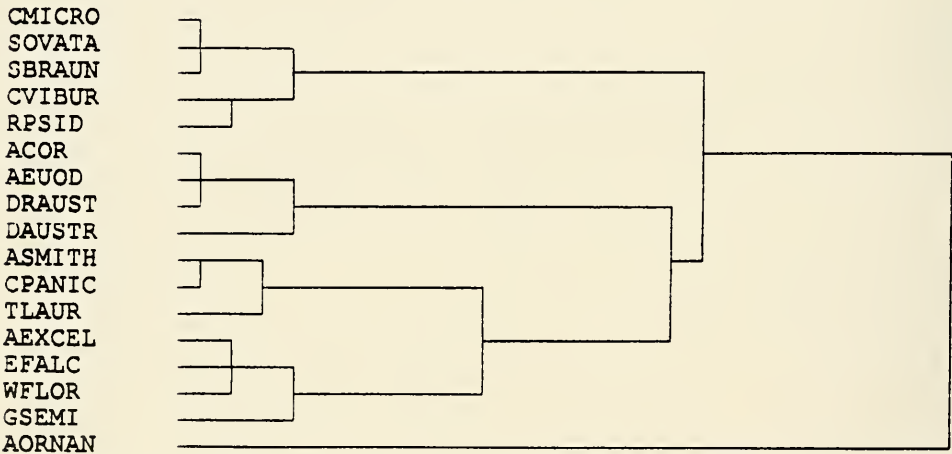


Fig. 2b



Figures 2a, 2b. Dendrograms of clustering of plant species on the basis of bee assemblages (a, all bee species; b, excluding *Apis*). Code: ACOR = *Alectryon coriaceus*, AEUOD = *Acradenia euodiiformis*, AEXCEL = *Alphitonia excelsa*, AORNAN = *Abrophyllum ornans*, ASMITH = *Acmena smithii*, CMICRO = *Cryptocarya microneura*, CPANIC = *Caldcluvia paniculosa*, CVIBUR = *Cutisia viburnea*, DAUSTR = *Diospyros australis*, DRAUST = *Drypetes australasica*, EFALC = *Euroschinus falcata*, GSEMI = *Guioa semiglauca*, RPSID = *Rhodomyrtus psidioides*, SBRAUN = *Scolopia braunii*, SOVATA = *Schizomeria ovata*, TLAUR = *Tristaniopsis laurina*, and WFLOR = *Waterhousea floribunda*.

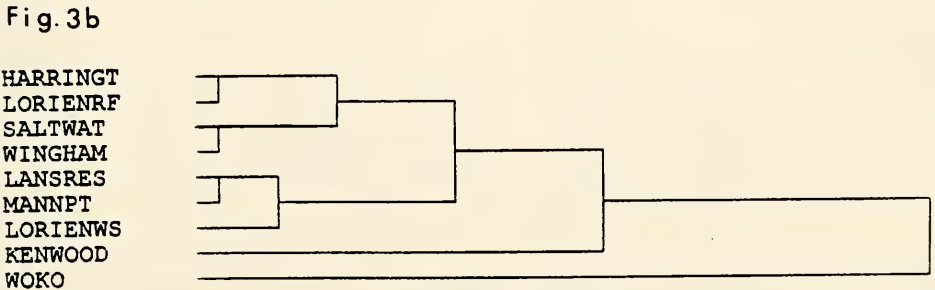
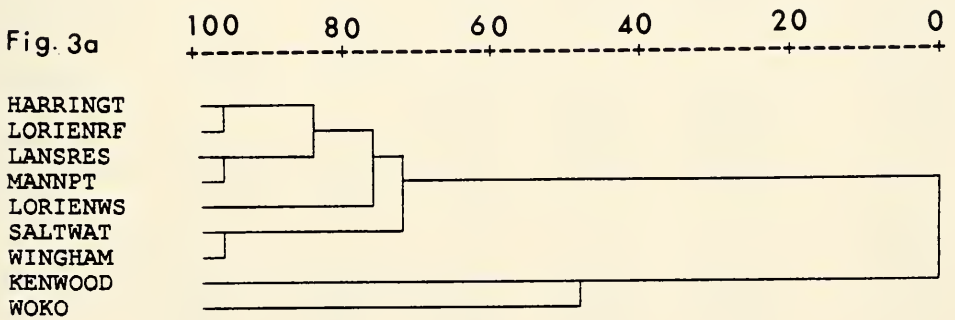
for completeness. No commercial *Apis mellifera* hives were located near the study sites and although honey bees may fly more than 8 km to forage (Roubik 1989, and references therein) all records for *Apis mellifera* are considered to be from feral populations. Although we did not attempt to locate and assess the number of feral colonies at any of the study sites estimates of feral *A. mellifera* hive density in tropical and semi-arid environments have been given as from 6 to more than 100 per km<sup>2</sup> (see Oldroyd et al. 1994).



The structure of the data in Table 1 was examined to determine whether plant species and/or sites could be characterised on the basis of assemblages of bee taxa. Agglomerative hierarchical cluster analysis (Ward's Method) was performed using the SPSS statistical package (Norusis/SPSS Inc. 1993). The raw data used were the number of bee species in each family, except for Colletidae, where subfamilies were recognised; data were standardised prior to analysis. Clustering was carried out both on the total data set and on the native species only (i.e., removing the widespread and abundant *Apis mellifera*).

Clustering of plant species (Figs 2a and 2b) showed that, in terms of bee utilisation, *Abrophyllum ornans* was very distinctive. This may reflect the small number of taxa recorded from the species, which was a function of the sampling technique. However, daily observation (x2) of *A. ornans* flowers (undertaken between 0730–2300 hrs), during the period of greatest flower availability, indicated that visits by bees were fewer than one every hour. The other plant species fall into a number of clusters (which differ in composition depending on whether *Apis* was included in the analysis). However, these clusters do not obviously reflect either taxonomy or flower morphology.

The site analysis (Figs 3a and 3b) indicates the presence of distinct assemblages of bees at Woko and Kenwood but the majority of sites are generally similar. The separation of the Woko assemblages, although collected from a single taxon (*Acmena smithii* var. 'minor'), is not surprising given that the site is at a higher elevation and further inland than the others. The general similarity of the Manning lowland sites suggests that within a limited geographic area stand structure and composition has a relatively minor influence on the bee assemblage.



Figures 3a, 3b. Dendrograms of clustering of study sites on the basis of bee assemblages (a, all bee species; b, excluding *Apis*). Code: HARRINGT = Harrington, KENWOOD = Kenwood Wildlife Refuge, LANSRES = Lansdowne Reserve, LORIENRF = Lorien Wildlife Refuge [rainforest site], LORIENWS = Lorien Wildlife Refuge [wet sclerophyll forest site], MANNPT = Manning Point, SALTWAT = Saltwater Reserve, WINGHAM = Wingham, WOKO = Woko National Park.

The observed recruitment and visitation of bees to most trees appeared to be greatly influenced by density of available blossoms. For example, trees of *Alectryon coriaceus* (Sapindaceae) possessing few flowers, or with many senescent flowers and developing fruit, were visited only occasionally by bees (usually *Exoneura* spp. or Hylaeinae). Isolated, often shaded, sparsely flowering *Acradenia euodiiformis* trees generally did not recruit bees even though densely flowering conspecific trees nearby were visited by large numbers of *Trigona carbonaria* and *Apis mellifera* (see Tables 2 and 3).

TABLE 2

Summary of bee recruitment to mass-flowering rainforest trees (plants listed alphabetically by family). Bees collected in netted samples; each daily record is derived from a composite of 10 inflorescence samples. Variation in number of daily samples and number of trees sampled is due to variation in flowering patterns. Number of native individuals: number of native taxa given in brackets "( )", number of *Apis mellifera* unbracketed. Samples collected during morning "m" or afternoon "a" indicated separately; "—" = no data/samples collected; "@\*" = approximate numbers only. Blossom: Leaf Surface ratio and relative estimate of Percentage Available open Buds indicated as "BLS:PAB"; "f" = no longer flowering.

## ANACARDIACEAE

*Euroschinus falcata***Harrington**

## male tree

date	19.11.90	26.11.90	3.12.90
m	18(0:0)	0(3:3)	1(0:0)
BLS:PAB	<40:<50	>40:<50	<10:f

## male tree

date	6.11.91	13.11.91	19.11.91
m tree1	23(17:@7)	0(2:2)	0(4:3)
a	0(7:2)	0(0:0)	0(1:1)
BLS:PAB	50:<50	40:50	40:>70

## male tree

date	6.11.91	13.11.91	19.11.91	26.11.91	2.12.91
m tree2	24(12:5)	6(0:0)	0(0:0)	0(0:0)	0(4:2)
a	—	0(1:1)	0(2:2)	0(0:0)	0(5:1)
BLS:PAB	50:<50	50:<10	40:<10	<50:<5	<30:>95

**Saltwater Reserve**

## female tree\*

date	12.11.91	19.11.91	26.11.91	3.12.91
m tree1	0(28:7)	8(16:8)	6(24:8)	0(1:1)
a	0(16:7)	6(4:4)	5(13:4)	0(0:0)
BLS:PAB	40:<5	50:30	50:>80	<30:100

\* not sampled 10.12.91 due to cessation of flowering

## male tree\*\*

date	19.11.91	26.11.91	3.12.91	10.12.91
m tree2	3(9:2)	0(56:4)	0(1:1)	0(5:2)
a	0(14:6)	0(7:4)	0(1:1)	0(2:2)
BLS:PAB	60:<5	>60:10	70:<10	60:<10

\*\* not sampled 12.11.91 due to lack of open flowers

**ESCALLONIACEAE***Cuttsia viburnea***Lorien Wildlife Refuge**

date	6.12.91	9.12.91	16.12.91	22.12.91
m	0(0:0)	0(6:3)	1(17:4)	1(0:0)
a	1(7:2)	0(2:1)	1(3:2)	0(0:0)
BLS:PAB	30:>50	30:>60	50:>90	50:100

date	12.12.92	23.12.92	28.12.92	
	no bees collected during this period			

**MYRTACEAE***Acmena smithii***Harrington**

date	19.11.90	26.11.90		
	19.11.92	27.11.92	7.12.92	14.12.92
	no bees collected during these periods			

**Lansdowne Reserve**

date	6.11.90	12.11.90	15.11.90
m	0(4:4)	0(5:3)	0(2:2)
BLS:PAB	>30:100	>60:100	<40:100

**Manning Point**

date	3.11.90	18.11.90	15.11.90
m tree1	0(10:5)	0(10:3)	0(1:1)
BLS:PAB	<40:<10	>40:—	>30:f

date	8.11.90	15.11.90
m tree2	0(10:3)	0(1:1)
BLS:PAB	>40:—	>70:f

**Woko National Park**

date	25.11.90	5.12.90
m tree1	0(0:0)	0(1:1)
a	1(5:5)	—
BLS:PAB	>30:<50	40:5

date	25.11.90	5.12.90
m tree2	0(0:0)	0(2:2)
a	1(1:1)	—
BLS:PAB	>30:>50	35:f

date	5.12.90
m tree3	0(1:1)
BLS:PAB	70:>50

*Tristaniopsis laurina***Wingham**

date	17.12.90	24.12.90
m tree1	0(2:2)	0(13:5)
BLS:PAB	<20:<50	30:60



date	17.12.90	24.12.90	(24.12.90, duplicate)
m tree2	0(0:0)	0(5:4)	0(18:8)
BLS:PAB	<20:>60	30:40	30:40

date	17.12.91	24.12.91
m tree1	7(1:1)	0(13:7)
a	1(1:1)	0(1:1)
BLS:PAB	10:>90	<10:100

date	24.12.91	2.1.92
m tree2	7(4:3)	4(9:6)
a	11(8:7)	1(10:9)
BLS:PAB	40:100	<30:100

date	2.1.92	7.1.92
m tree3	0(11:5)	4(10:4)
a	0(22:13)	3(4:4)
BLS:PAB	40:100	<30:100

**Lorien Wildlife Refuge**

date	26.12.91	3.1.92	6.1.92
m	1(10:9)	0(3:3)	0(5:1)
a	2(9:6)	0(27:@20)	1(4:3)
BLS:PAB	30:>40	40:80	40:>90

*Waterhousea floribunda***Wingham**

date	14.11.90	22.11.90	29.11.90
m tree1	5(16:7)	5(10:5)	1(8:4)
BLS:PAB	<30:<30	40:>95	<20:f

date	22.11.90	29.11.90	6.12.90
m tree 2	0(30:@6)	1(14:8)	1(20:10)
BLS:PAB	>50:>90	>60:>70	10:f

date	19.11.91	27.11.91	3.12.91	10.12.91
m tree1	6(18:5)	0(2:2)	4(15:7)	0(2:1)
a	2(25:15)	3(10:8)	8(4:4)	1(1:1)
BLS:PAB	60:50	>70:>90	60:100	<10:100

date	19.11.91	27.11.91	3.12.91	10.12.91	17.12.91
m tree2	2(7:5)	6(5:4)	7(11:5)	3(50:11)	20(11:8)
a	2(9:6)	7(7:6)	9(12:8)	5(9:7)	3(17:9)
BLS:PAB	50:45	70:45	70:50	>70:>90	<20:100

date	17.12.91	24.12.91
m tree3	1(18:7)	2(18:9)
a	3(6:6)	1(5:3)
BLS:PAB	70:100	70:100

**Lorien Wildlife Refuge**

date	1.12.90
m	1(0:0)
BLS:PAB	>50:>50

date	29.11.91	5.12.91
m tree1	2(29:18)	0(1:1)
a	3(23:4)	1(10:5)
BLS:PAB	30:50	<30:>90
date	29.11.91	5.12.91
m tree2	3(24:16)	2(11:6)
a	1(20:11)	3(17:13)
BLS:PAB	30:70	40:>90

**RHAMNACEAE***Alphitonia excelsa***Harrington**

date	3.1.91	11.1.91	19.1.91	25.1.91	1.2.91	cont.
m tree1	0(0:0)	0(0:0)	0(0:0)	0(0:0)	1(0:0)	
BLS:PAB	>30:<1	40:<30	40:50	30:<40	30:>80	

date	9.2.91	14.2.91	22.2.91
m tree1	1(0:0)	0(0:0)	0(0:0)
BLS:PAB	30:>90	<30:f	<10:f

date	3.1.91	11.1.91	19.1.91	25.1.91	1.2.91	cont.
m tree2	0(0:0)	0(0:0)	1(0:0)	2(0:0)	1(0:0)	
BLS:PAB	>30:<5	40:<30	60:>50	50:>50	<40:>70	

date	9.2.91	14.2.91	22.2.91
m tree2	1(0:0)	0(0:0)	0(0:0)
BLS:PAB	20:f	<10:f	30:>90

date	3.2.92	12.2.92	20.2.92	28.2.92	6.3.92	12.3.92
m tree1	0(0:0)	3(0:0)	39(0:0)	11(1:1)	0(0:0)	0(0:0)
a	1(0:0)	12(2:2)	38(0:0)	9(0:0)	9(0:0)	0(0:0)
BLS:PAB	30:<10	50:30	>50:>60	50:90	30:>99	<10:f

date	3.2.92	12.2.92	20.2.92	28.2.92	6.3.92	12.3.92
m tree2	2(0:0)	15(1:1)	63(1:1)	24(0:0)	14(0:0)	0(0:0)
a	0(0:0)	21(0:0)	20(0:0)	18(0:0)	16(0:0)	0(0:0)
BLS:PAB	30:<10	40:30	>50:>50	>60:>95	40:>95	<20:f

date	28.1.93	4.2.93	11.2.93	1.3.93
m tree1	3(16:1)	9(14:1)	2(17:1)	1(0:0)
a	0(1:1)	6(9:1)	1(5:1)	0(0:0)
BLS:PAB	40:20	40:30	—	<10:80

date	28.1.93	4.2.93	11.2.93	1.3.93
m tree2	0(0:0)	0(0:0)	2(6:1)	3(0:0)
a	0(8:1)	2(7:1)	4(3:2)	2(0:0)
BLS:PAB	<20:<10	<20:<20	—	<30:>90

**Kenwood Wildlife Refuge**

date	6.2.92	13.2.92	22.2.92	29.2.92
m tree1	3(0:0)	2(0:0)	0(0:0)	5(0:0)
a	4(0:0)	4(0:0)	14(2:2)	6(2:2)
BLS:PAB	30:<5	<30:<20	40:50	30:>90

date	6.2.92	13.2.92	22.2.92	29.2.92
m tree2*	15(0:0)	0(0:0)	0(0:0)	0(0:0)
a	1(2:1)	17(9:4)	10(0:0)	1(0:0)
BLS:PAB	40:20	40:>60	30:>90	30:>90

\* tree shaded each morning

## RUTACEAE

*Acradenia euodiiiformis*

### Lorien Wildlife Refuge

date	18.9.91	19.9.91	25.9.91	2.10.91
0800hrs	—	2(0:0)	0(0:0)	0(0:0)
1000hrs	8(8:5)	13(8:3)	6(29:5)	0(10:5)
1200hrs	10(10:6)	—	7(43:5)	0(9:3)
1400hrs	3(3:1)	—	9(69:6)	0(3:1)
1600hrs	1(0:0)	—	0(13:3)	0(0:0)
1800hrs	0(0:0)	—	0(0:0)	0(0:0)
2000hrs	0(0:0)	—	0(0:0)	0(0:0)
BLS:PAB	50:35	“	60>70	50:<5

## SAPINDACEAE

*Alectryon coriaceus*

### Manning Point

date	17.12.91	27.12.91
m tree1	0(19:<8)	0(2:1)
a	0(1:1)	0(0:0)
BLS:PAB	40:f	30:f

date	27.12.91	2.1.92
m tree3	3(17:@4)	2(0:0)
a	1(0:0)	1(1:1)
BLS:PAB	40:50	50:f

date	2.1.92
m tree4	2(5:@2)
a	3(2:1)
BLS:PAB	50:f

### Harrington

date	7.1.93	11.1.93	18.1.93
m tree1	0(0:0)	3(3:1)	2(0:0)
a	2(0:0)	1(0:0)	1(0:0)
BLS:PAB	<30:>60	40:>70	>30:>70

date	7.1.93	11.1.93	18.1.93
m tree2	1(0:0)	2(1:1)	1(0:0)
a	1(0:0)	3(1:1)	1(0:0)
BLS:PAB	<30:>60	<20:>70	<20:100

*Guioa semiglauca*

### Harrington

date	6.11.90	12.11.90	19.11.90	26.11.90	3.12.90
m tree1	1(0:0)	22(0:0)	60(0:0)	66(0:0)	27(0:0)
a	—	—	6(1:1)	—	—
BLS:PAB	—	50:—	>50:>80	50:>80	>20:>90



date	6.11.90	12.11.90	19.11.90	26.11.90
m tree2	15(0:0)	36(0:0)	23(0:0)	39(0:0)
a	—	4(1:1)	—	—
BLS:PAB	—	50:40	<70:>50	<60:—
date	26.11.90			
m tree3	5(1:1)			
BLS:PAB	60:>40			
date	19.11.92	27.11.92	7.12.92	14.12.92
m tree1	0(0:0)	2(3:1)	31(8:2)	3(0:0)
a	0(1:1)	0(0:0)	0(5:1)	0(0:0)
BLS:PAB	<10:<5	<30:<20	<20:>80	<10:100
date	14.12.92	21.12.92	25.12.92	
m tree2	6(0:0)	1(1:1)	2(1:1)	
a	5(1:1)	0(0:0)	1(0:0)	
BLS:PAB	<10:<20	<10:50	<10:100	

The abundance of individuals was generally highest during peak flowering, but the peak in abundance is more pronounced in relation to BLS than PAB (Tables 2 and 3, Figs 4c and 4d). There were no clear trends in the number of species in relation to availability of resources (Figs 4c and 4d), although over the season numbers of individuals and species show a similar pattern with peaks in November/December (Figs 4a and 4b). Floral morphology did not appear to strongly influence recruitment. High numbers of visiting bee taxa were obtained from *Euroschinus falcata* (13 spp. Harrington–20 spp. Saltwater), *Acradenia euodiiformis* (16 spp. Lorien), *Tristaniopsis laurina* (31 spp. Lorien–24 spp. Wingham) and *Waterhousea floribunda* (22 spp. Lorien–30 spp. Wingham) (Table 1). These trees include species both with open dish-like corollas with half inferior ovaries (*T. laurina*, *W. floribunda*) and those with superior ovaries (*E. falcata*, *A. euodiiformis*). The latter group are often visited by eusocial Apidae whilst unadapted or semi-specialised (see Faegri and van der Pijl 1979) Colletidae characterise the bee visitors to the former. The greatest cumulative number of bee species was collected from *Tristaniopsis laurina* (46 spp.) and *Waterhousea floribunda* (41 spp.) (Table 1). However, both species were sampled at the Wingham and Lorien sites, which also possessed the richest bee faunas (Tables 1 and 2), and the high bee numbers recorded for *T. laurina* and *W. floribunda* may reflect site influences.

Approximately 80 percent ( $n=78$ ) of the bee records were from three or fewer plant species or individual locations (Table 1). Only *Heterapoides* sp. near *exleyae* (Colletidae) and the introduced honey bee *Apis mellifera* (Apidae) were recorded from 10 or more of the plants sampled. *Apis mellifera* was collected from all but five plant species (*Caldcluvia paniculosa*, *Schizomeria ovata*, *Abrophyllum ornans*, *Drypetes australasica*, *Cryptocarya microneura*; *Apis mellifera* was recorded from sites at which these species were in flower), which nevertheless, do not possess flowers, flowering strategies, or offer floral resources of a nature that would appear to preclude *Apis* foraging. The bee fauna of individual tree species frequently differed between sites, and these differences were expressed both where trees were sampled in floristically and topographically different forests (e.g., *Tristaniopsis laurina* at Wingham Brush and Lorien Wildlife Refuge), as well as floristically related subformations (e.g., *Euroschinus falcata* in littoral rainforests at Harrington and Saltwater Reserve).

TABLE 3

Changes in bee activity on *Acradenia euodiiformis* (Lorien Wildlife Refuge) during the course of the day. Key to weather conditions: C=cold; f=scattered clouds; R=rain; T=twilight; c=cool; h=warm-hot; S=sunny; W=gusting, strong winds; d=dark; H=very hot; s=dappled light on tree; w=light wind, breeze; F=fine; HU=humid; sh=tree shaded.

	800	1000	1200	1400	1600	1800	2000	/	800	1000
<b>18-19.9.91</b>										
<b>No. of individuals</b>										
<i>Apis mellifera</i>	—	8	10	3	1	0	0		2	13
<i>Trigona carbonaria</i>	—	4	6	3	0	0	0		0	6
misc. native bees	—	4	5	0	0	0	0		0	2
total bees	—	16	21	6	1	0	0		2	21
total insects (incl. bees)	—	88	112	71	143	412	93		75	105
<b>No. of taxa</b>										
other Apoidea	—	4	5	0	0	0	0		0	2
total bees	—	6	7	2	1	0	0		2	4
total insects (incl. bees)	—	38	47	41	60	72	40		47	47
BLS:PAB 50:>30										
weather condition	n/a	sWF	SWF	SWF	shWF	CWFT	cwF		sCw	Sf
<b>25.9.91</b>										
<b>No. of individuals</b>										
<i>Apis mellifera</i>	0	6	7	9	0	0	0			
<i>Trigona carbonaria</i>	0	23	35	57	10	0	0			
misc. native bees	0	6	8	12	3	0	0			
total bees	0	35	50	78	13	0	0			
total insects (incl. bees)	142	280	259	284	190	198	182			
<b>No. of taxa</b>										
other Apoidea	0	4	4	5	2	0	0			
total bees	0	6	6	7	3	0	0			
total insects (incl. bees)	31	46	44	42	43	40	22			
BLS:PAB 60:>70										
weather condition	cshF	sf	Swh	Sshw	shcwf	cwT	cWd			
<b>02.10.91</b>										
<b>No. of individuals</b>										
<i>Apis mellifera</i>	0	0	0	0	0	0	0			
<i>Trigona carbonaria</i>	0	2	4	3	0	0	0			
misc. native bees	0	8	5	0	0	0	0			
total bees	0	10	9	3	0	0	0			
total insects (incl. bees)	271	86	30	69	35	83	71			
<b>No. of taxa</b>										
other Apoidea	0	4	2	0	0	0	0			
total bees	0	5	3	1	0	0	0			
total insects (incl. bees)	37	18	17	18	10	11	16			
BLS:PAB 50:<5										
weather condition	cshF	Shw	SHw	SshHW	shcW	cfwT	Fd			

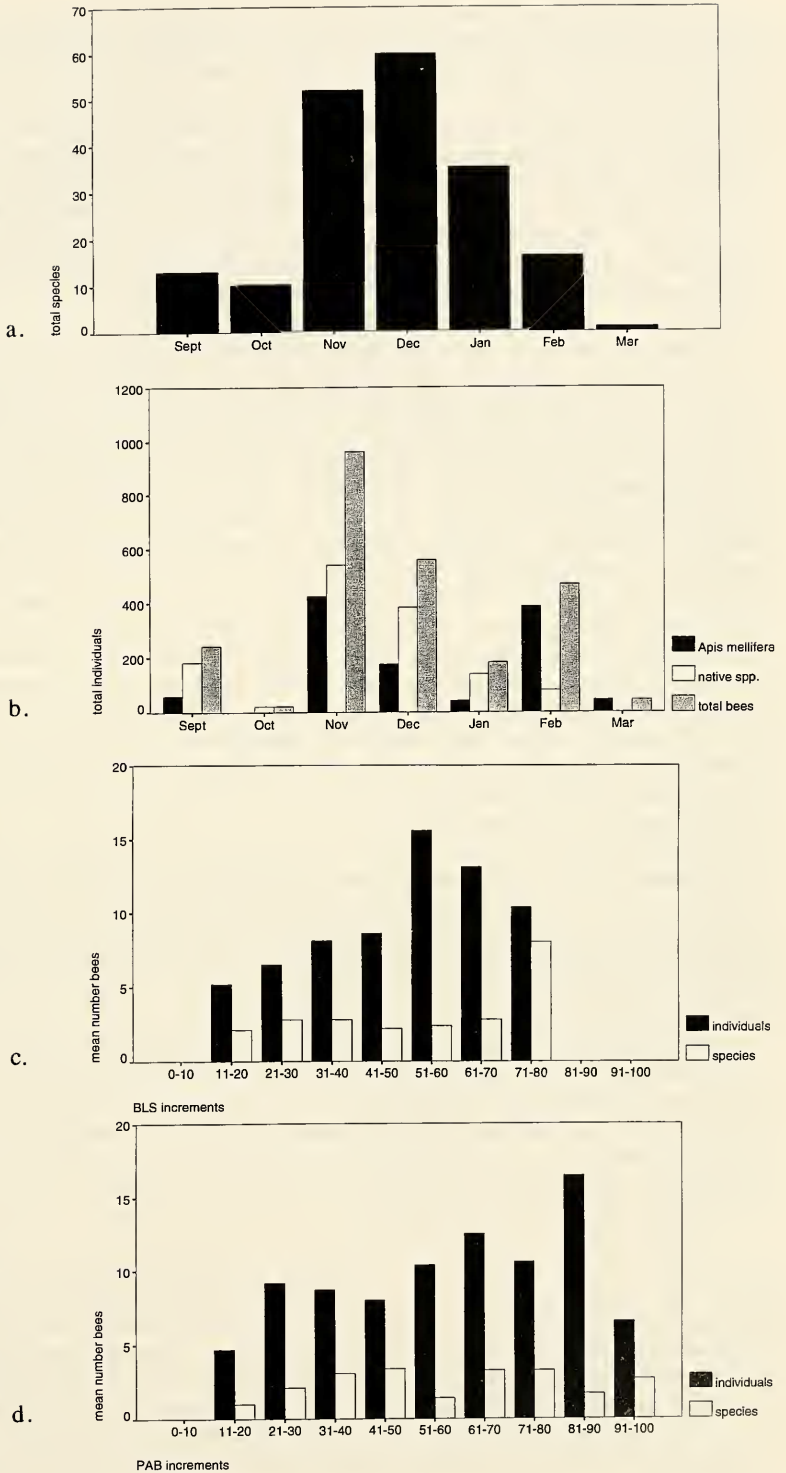


Figure 4. a). Monthly numbers of bee species, b). Monthly numbers of bee individuals, c). Mean number bee taxa and individuals in 10% increments of BLS, d). Mean number bee taxa and individuals in 10% increments of PAB.

At both the family and generic level bees exhibited a broad polytropic response within the spectrum of trees sampled (Table 1). However, more extensive sampling is required to assess the plant fidelity of individual bee species to particular plant species. Where bee genera were recorded from single, or few, plant species this may be due to actual rarity in rainforest, rather than a close plant-pollinator mutualism. Conversely, if populations of individual bee taxa occur (or forage) as spatial or temporal mosaics within rainforest communities then our sampling may have biased against their collection.

Anthophoridae were collected from Ebenaceae, Euphorbiaceae, Myrtaceae, Rhamnaceae, Rutaceae and Sapindaceae but many of these records are represented solely by the genus *Exoneura*. At least two anthophorid genera, *Lestis* and *Amegilla*, foraged in a traplining manner (see Janzen 1971; Roubik 1989; Gross 1993) (G. Williams pers. observ.).

Only two apids occur in the region; introduced *A. mellifera* and the native *Trigona carbonaria*. *Apis mellifera* can dominate the flower-frequenting insect fauna in fragmented forests (Aizen and Feinsinger 1994), competes with native pollinators for floral resources (Anderson 1989), and may modify the pollination ecology of native plants (Pyke and Balzer 1982; Paton 1985; Pyke 1990; Sugden and Pyke 1991). *Apis mellifera* was common at all sites and foraged on species of Anacardiaceae, Ebenaceae, Escalloniaceae, Flacourtiaceae, Myrtaceae, Rhamnaceae, Rutaceae and Sapindaceae. However, *A. mellifera* generally restricted its foraging activity to inflorescences in full sunlight. *Trigona carbonaria* was collected from fewer tree taxa (Anacardiaceae, Escalloniaceae, Myrtaceae, Rhamnaceae, Rutaceae) but did not forage on mass-flowering *Waterhousea floribunda* at Wingham and Lorien Wildlife Refuge even though it commonly foraged at other mass flowering trees at these sites. *Trigona carbonaria* was recorded from only one littoral rainforest site (Saltwater Reserve) where it co-foraged with *A. mellifera* on *Euroschinus falcata* flowers. *Trigona* species have not been recorded from two other littoral rainforest sites, Harrington and Manning Point, which have been subject to intensive invertebrate surveys since 1975 (Williams 1993). *Trigona carbonaria* generally only foraged at large or concentrated blossom resources, rather than isolated blossoms or inflorescences.

Halictidae were recorded from Anacardiaceae, Cunoniaceae, Ebenaceae, Euphorbiaceae, Flacourtiaceae, Myrtaceae, Rhamnaceae, Rutaceae and Sapindaceae. However, of the two principal halictid genera, *Homalictus* and *Lasioglossum*, individuals of *Homalictus* are more abundant at littoral rainforest sites and are common foragers on the flowers of many adjoining dune plants (e.g., *Scaevola*, *Hibbertia*). *Lasioglossum* is a distinctive and characteristic genus of the bee fauna of mass-flowering Myrtaceae in lowland rainforests.

Megachilidae were more restricted in their occurrence and were only collected from Ebenaceae, Escalloniaceae and two species of Myrtaceae (*Tristaniopsis laurina*, *Waterhousea floribunda*). Megachilids were encountered as either occasional 'rare' visitors or as episodic 'flushes' of larger numbers of taxa and individuals at single peak-flowering trees, such as at Lorien Wildlife Refuge in January 1991 when large numbers of *Chalicodoma lucidiventris* and *Megachile* spp. occurred on *T. laurina* during a three day period of peak flower availability.

Of the families collected Colletidae were represented by the largest number of species but a number of genera were restricted in ecological and geographic range within the study area. *Paracolletes* (Colletinae), *Pachyprosopis* and *Sericogaster* (Euryglossinae) and *Palaeorhiza* (Hylaeinae) were only collected in riverine and riparian rainforests and their adjoining ecotones. *Meroglossa* (Hylaeinae) was only recorded from a rainforest ecotone at the Lorien site. Most Colletinae, predominantly species of *Leioproctus*, were collected from Myrtaceae, but were also recorded from Anacardiaceae, Escalloniaceae, Rhamnaceae, Rutaceae and Sapindaceae. Euryglossinae were principally collected on Myrtaceae and, with the exception of *Euryglossa*,



*Euryglossella* and *Euryglossina* species from Saltwater Reserve, were otherwise not collected from littoral rainforest. High species richness of *Euryglossa* (Euryglossinae), in combination with *Leioproctus* (Colletinae), was a characteristic of the *Waterhousea floribunda* bee fauna.

Hylaeinae, principally species of *Hylaeus*, contained the greatest number of species (Table 1) and characterised the native bee fauna of mass-flowering littoral rainforest trees. The greatest number of hylaeine species was recorded in rainforest remnants at Harrington, Wingham and Lorien Wildlife Refuge (Table 1) but this may reflect the greater numbers of samples collected at these three sites. The subfamily was recorded from all plant families but was particularly numerous on Myrtaceae. Most genera appear to be polytropic, at best, oligotropic, in their fidelity to mass-flowering rainforest plants and *Heterapoides* and *Hylaeus*, in particular, were collected from a broad spectrum of flowering rainforest trees (12 and 13 spp. respectively) (Table 1). However, Hylaeinae were not observed on specialised (e.g., Orchidaceae) or semi-specialised (e.g., Commelinaceae, Zingiberaceae, Papilionaceae) zygomorphic rainforest plant flowers examined opportunistically at the study sites. Hylaeinae were often the only bees observed visiting isolated, partially shaded or understorey flowers of otherwise massed, crown-flowering rainforest trees. *Hemirhiza melliceps*, for example, preferentially foraged on shaded, often isolated, flowers of *Alectryon coriaceus* (Sapindaceae) and *Diospyros australis* (Ebenaceae). *Palaeorhiza* sp. also foraged on shaded *D. australis* flowers. Consequently, hylaeine species may contribute to pollination of spatially-restricted, small blossom clusters.

In addition to the hylaeine records given in Table 1 two species of the genus *Hyleoides* were observed in the study region. *Hyleoides* sp. near *concinna* visited flowers of *Brachychiton acerifolius* (Sterculiaceae) (at Coocumbac Island Nature Reserve, Taree) and *Hyleoides concinna* foraged on orchard plantings of exotic pomegranate *Punica granatum* (Punicaceae) at Lorien Wildlife Refuge. Both plants possess vivid red flowers that, although broadly 'tubular' in shape, possess no obvious nectar guides and are readily accessible to bees. The two *Hyleoides* records are particularly interesting because they indicate foraging constancy (neither species was observed on other flowering plants) and represent a departure from the 'bird' pollination syndrome (see Williams and Adam 1994) suggested by the red-coloured flowers of *B. acerifolius* and *P. granatum*. Additionally, bees have an inability to see red (Barth 1991).

Hylaeine visitation to a phylogenetically diverse mass-flowering subtropical rainforest flora follows the broad polytropic response by Hylaeinae, and Colletidae generally, to plant species in less mesic habitats (see records in Houston 1975, 1981; Armstrong 1979). The unifying theme of plant visitation by Hylaeinae appears to be one of blossom morphology, rather than shared phylogeny, in which visited plant species generally possess allophilic (with no structural characters for guiding visitors) or hemiphilic (intermediately adapted) blossoms (see Faegri and van der Pijl 1979) capable of being pollinated by relatively short-tongued and semi-specialised anthophilous insects. The ecological distribution of Hylaeinae appears to be diverse, and hylaeines represent a potential source of generalist pollination vectors upon which rainforest trees with unspecialised 'generalist' pollination requirements may be able to draw.

### **Influence of flower availability on bee activity**

Bees respond to increased availability of floral resources (Augspurger 1980; Roubik 1989). The greatest numbers of bee species and individuals were recorded in November and December (Table 1, Figs 4a and 4b) a period when a greater number of tree species were sampled. The numbers recorded for February and March (Figs 4a and 4b) are largely derived from *Alphitonia excelsa*.

The bee data from 2-hourly netted inflorescence samples of *Acradenia euodiiformis*,

and selected daily samples from other flowering trees (due to absence of bees in some samples, and very short flowering periods of some plant species) are summarised in Tables 2 and 3.

Abundance and diversity of bees were influenced by daily changes in weather conditions (e.g., cloudiness, wind, and possibly increases in temperature) but increased foraging frequency by individuals and increased number of bee species at flowers was generally associated with increased blossom to leaf surface ratios (BLS) and increased bud opening (PAB) (Tables 2 and 3, Figs 4c and 4d). Decreased foraging frequency and reduction in taxonomic diversity of the bee fauna generally corresponded with reduction in available floral resources reflected in decreases in BLS ratios as a result of reduction or senescence of available blossoms — this being a direct consequence of floret abscission and senescence.

Diel responses by bees, with maximal recruitment patterns generally between 1000–1400 hrs, are seen in data for *Acradenia euodiiformis* (Table 3); the patterns of all bees are concordant in terms of trends in daily abundance (i.e. *Apis*, *Trigona* and other native bees). The visitation of other insects to *A. euodiiformis* varied over longer daily time periods but there seemed to be no consistency in the abundance patterns of total insects (including bees) (Table 3). *Apis mellifera* foraging is maximal at mid to peak-phase while *Trigona carbonaria* and other native bees commence or continue to forage during diminished resource phases (Table 3). Similarly, *Trigona* foraged on late phase *Archontophoenix cunninghamiana* flowers in March 1993 at Lorien Wildlife Refuge when *A. mellifera* numbers were greatly reduced.

Data for *Euroschinus falcata*, *Guioa semiglauca*, *Waterhousea floribunda*, *Tristaniopsis laurina* and *Alphitonia excelsa* (Table 2), species exhibiting longer flowering periods, also demonstrate fluctuations in bee frequency and diversity that generally corresponded with increases and reductions in available floral resources. Reduced abundance of bees in these samples also corresponded with onset of rain or shading of the tree crown during part of the day.

Additionally, preferential visitation to particular trees within populations and, in dioecious spp. (e.g., *E. falcata*), preferential foraging at either female or male plants was observed. At the Saltwater site on the 26th November 1991 *Trigona carbonaria* was common on male *E. falcata* trees but *Apis mellifera* was absent. In contrast, *Apis* was very common throughout the day at the single flowering female tree. *Apis mellifera* was absent or an uncommon forager at male flowers throughout the sampling of *E. falcata* at Saltwater Reserve. *Trigona carbonaria* foraged in large numbers at both male and female trees, and significantly (for potential pollination contributions) foraged at both male and female trees throughout the *E. falcata* flowering episode.

Concentration of *Apis* foraging activity, within peak flowering periods, was also marked in *Alphitonia excelsa* (1992, 1993) and *Guioa semiglauca* (1990, 1992) at Harrington (Table 2). Relative foraging constancy by *A. mellifera*, however, occurred throughout the flowering period of *Waterhousea floribunda* at both the Wingham and the Lorien sites. *Apis* showed no preferential foraging at *Tristaniopsis laurina*, being frequently absent in samples, contrary to the putative bee adaptation suggested by the yellow colouration of its flowers.

### **Interaction between *Apis mellifera* and *Trigona carbonaria***

Interactions between the eusocial apids *Apis mellifera* and *Trigona carbonaria* are of interest because of the possible resource competition between the two species and the potential for displacement of native 'stingless' bees (*Trigona* and *Austroplebeia* spp., Cardale 1993) by feral *Apis* populations.

*Apis mellifera* is recorded as a common visitor to tropical, subtropical and cool temperate Australian rainforest plants (Hopper 1980; House 1985; Crome and Irvine



1986; Ettershank and Ettershank 1990; Gross 1993; Heard 1993) and honey bees were common at all our study sites. During this study *Trigona carbonaria* was sampled from *Euroschinus falcata* (Saltwater), *Rhodomirtus psidioides*, *Abrophyllum ornans*, *Acradenia euodiiformis* (Lorien Wildlife Refuge), *Tristaniopsis laurina* (Wingham), *Alphitonia excelsa* (Kenwood Wildlife Refuge), and possibly *Cuttsia viburnea* (Lorien Wildlife Refuge) (see Table 1), but was common only on *E. falcata* and *A. euodiiformis* flowers. *Trigona carbonaria* was also common ( $>10 \text{ m}^{-2}$ ) at *Archontophoenix cunninghamiana* (Arecaceae) flowers at Lorien Wildlife Refuge and synchronously, mass-flowering *Austrosteenisia blackii* (Papilionaceae) vines in the riverine rainforest remnant at Lansdowne Reserve.

Interaction was observed between *A. mellifera* and other native bee genera. Foraging activity of *Apis mellifera* readily disturbed co-foraging native Hylaeine (which flew off when touched by *Apis*) on all occasions when *Apis* and hylaeines were present on flowers. Ettershank and Ettershank (1990) noted reduced native insect numbers near Tasmanian bee-keeping sites but did not observe interactions between native insects and *Apis*.

No direct interaction, displacement or avoidance movement between introduced *Apis* and native *Trigona* bees was observed during fieldwork. Although there are considerable differences in size between the species (*Apis*  $>9$  mm, *Trigona*  $<6$  mm) *Trigona* individuals continued to forage, apparently undisturbed by the presence of *Apis*. These observations, however, were made when *Apis* occurred at only moderate numbers (approx.  $<10 \text{ m}^{-2}$ ) or when *Apis* exhibited preferential visitation to single-sexed trees in dioecious populations as on *E. falcata* at Saltwater.

Additional observations (over a number of seasons since 1991) also suggest an absence of displacement or interference interactions between *Apis* and *Trigona* on *Cordyline stricta* (Agavaceae), *Alocasia brisbanensis* (Araceae), *Archontophoenix cunninghamiana* (Arecaceae), arboretum plantings of male *Rhodospaera rhodanthema* (Anacardiaceae) and domestic and horticultural crops adjoining the Lorien study site, and on plantings of *Banksia ericifolia* (Proteaceae) at Bulahdelah in 1991 (G. Williams pers. observs.).

This apparent lack of disturbance or displacement of *Trigona* cannot be interpreted as evidence for no adverse impact from the foraging of introduced *Apis mellifera* on other native pollinators. McAlpine (1988) notes disturbance by *Apis mellifera* of *Trigona* ?*carbonaria* and *Neurochaeta inversa* (Diptera) taking pollen from *Alocasia brisbanensis* (as *A. macrorrhiza*) in southeast Queensland. *Apis* readily disturbed the foraging activities of native Diptera (i.e. Syrphidae, Lauxaniidae, Drosophilidae) and Coleoptera (Nitidulidae, Chrysomelidae, Scirtidae) on flowering *Archontophoenix cunninghamiana* palms at Lorien Wildlife Refuge and native insects generally on flowering *Guioa semiglauca* trees at Harrington (G. Williams pers. observ.). *Apis mellifera* may compete with native fauna for nest hollows (Oldroyd et al. 1994) and, as suggested elsewhere (Williams 1993), critical population displacement of *Trigona* may occur at prospective hive/nest sites (i.e. tree hollows) rather than the food source. *Trigona* may be particularly vulnerable at nest establishment because founding of *Trigona* colonies is by way of initial establishment by young queens in concert with small numbers of workers rather than the massed swarms utilised by *Apis* (Michener and Houston 1991). Such small founding colonies are potentially readily overwhelmed. Additionally, old *Trigona* queens are unable to vacate nests, as can *Apis* queens (Michener and Houston 1991), so that destruction or loss of nest sites (e.g., through fire) may involve loss of the hive's means of re-establishment at an alternative site.

Managing rainforest so as to preserve or sustain a diverse pollinator guild may be critical to the long-term viability of individual plant populations and the ecosystem in general. A diverse pollinator guild may be important in that it provides flexibility and resilience in breeding systems in the face of environmental change (Williams and Adam

1994). Williams and Adam (1994) suggest that a reduction in the total pollinator guild may result in the loss of subsets of species required for pollination of particular plants.

Potential threats to pollinator guild diversity (and flexibility in plant reproductive ecology) are posed by the increasing fragmentation of habitat and the monopolising of floral resources, important to some pollinators, by introduced *Apis mellifera*. Although there is always a large array of anthophilous insects on subtropical rainforest trees, within which native bees are not a numerically dominant element, bees may nevertheless play an important role in pollination ecology in rainforests.

### ACKNOWLEDGMENTS

Dr Terry Houston (Western Australian Museum, Perth), Mr Ken Walker (Museum of Victoria, Melbourne), Drs Ian Naumann and Josephine Cardale (CSIRO, Canberra), Dr Judy King (Queensland Forest Service, Brisbane), Dr David McAlpine, Dr Graham Pyke and Colleen Pyne (The Australian Museum, Sydney), and Dr Glynn Maynard (A.B.R.S., Canberra) kindly provided identifications or helped with reference material. Debbie Stevenson (University of NSW) is thanked for help with manuscript preparation. Dr M. Gray (Australian Museum) is thanked for comments on an earlier draft of the manuscript and the National Parks and Wildlife Service (NSW) is thanked for permission to undertake studies in Woko National Park. One of us (G.W.) thanks the Australian Museum for receipt of an Australian Museum Postgraduate Research Grant and the Australian Entomological Society Inc. for a grant in aid of research.

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## APPENDIX

**Range extension records**

A number of bee species collected from the study sites represent new distribution records and are listed below.

**Colletidae**

*Callomelitta ?fulvicornis*. *C. fulvicornis* is known only from type locality 'Jamberoo' (NSW) (Cardale 1993).

*Euryglossa terminata*. Only published localities 'Brisbane, near Emu Vale (Qld), and Patonga (NSW)' (Cardale 1993).

*Hemirhiza melliceps*. Previously recorded from southern Queensland (Cardale 1993).

*Hylaeus amiculiformis*. Previous published records 'Mackay, Brisbane' (Qld) (Cardale 1993).

*Hylaeus amicus*. Recorded from Western Australia, South Australia, Victoria and western New South Wales (Cardale 1993); range extension to northern New South Wales.

*Hylaeus cyanophilus*. Only published records 'Mackay, Redlynch and Goodna' (Qld) (Cardale 1993).

*Hylaeus foveatus*. Only published localities Jamberoo and Lorne, New South Wales (Cardale 1993).

*Hylaeus jacksoniae*. Only published localities Mt Coot-tha (Brisbane, Qld) and 'near Woodenbong' (NSW) (Cardale 1993).

*Hylaeus micropheanax*. Previously only known from type locality 'Mackay' (Cardale 1993).

*Hylaeus primulipictus*. Known only from type locality 'Mackay' (Qld) (Cardale 1993).

*Hylaeus proximus*. Recorded from Murray-Darling Basin (NSW?), South Australia and Western Australia (Cardale 1993).

*Palaeorhiza* sp.. Probable new species (T. Houston pers. comm.), genus previously recorded from Queensland and Northern Territory (Cardale 1993).

*Sericogaster fasciata*. Only published localities 'Mackay, Birkdale, near Stanthorpe [Qld] and Gosford [NSW]' (Cardale 1993).

**Halictidae**

*Lasioglossum polygoni*. Range extension from Noosa (Qld) (K. Walker pers. comm.).

**Megachilidae**

*Chalicodoma punctata*. Previously only recorded from 'New Holland', exact distribution unknown (Cardale 1993).

*Megachile deanii*. Range extension from southern Queensland (Cardale 1993).

*Megachile pictiventris*. Range extension from far north coast, New South Wales (Cardale 1993).